

PRESERVATION OF FISH IN THE CRETACEOUS SANTANA FORMATION OF BRAZIL

by DAVID M. MARTILL

ABSTRACT. Early diagenesis of calcareous concretions in the Santana Formation (Cretaceous) of north-east Brazil has allowed some fishes killed in mass mortality events to be preserved three dimensionally. Fluctuating salinities may have been responsible for the mass deaths of the dominantly marine fish fauna. Early phosphatization, brought about by bacterial activity, has allowed a variety of soft tissues to be preserved within the body cavity of a variety of fish taxa. Both high and low pH micro-environments existing within the body cavity of the fishes allowed the precipitation of microcrystalline francolite within the partly decomposing soft tissues, while early non-ferroan calcite was produced within the coelomic cavity.

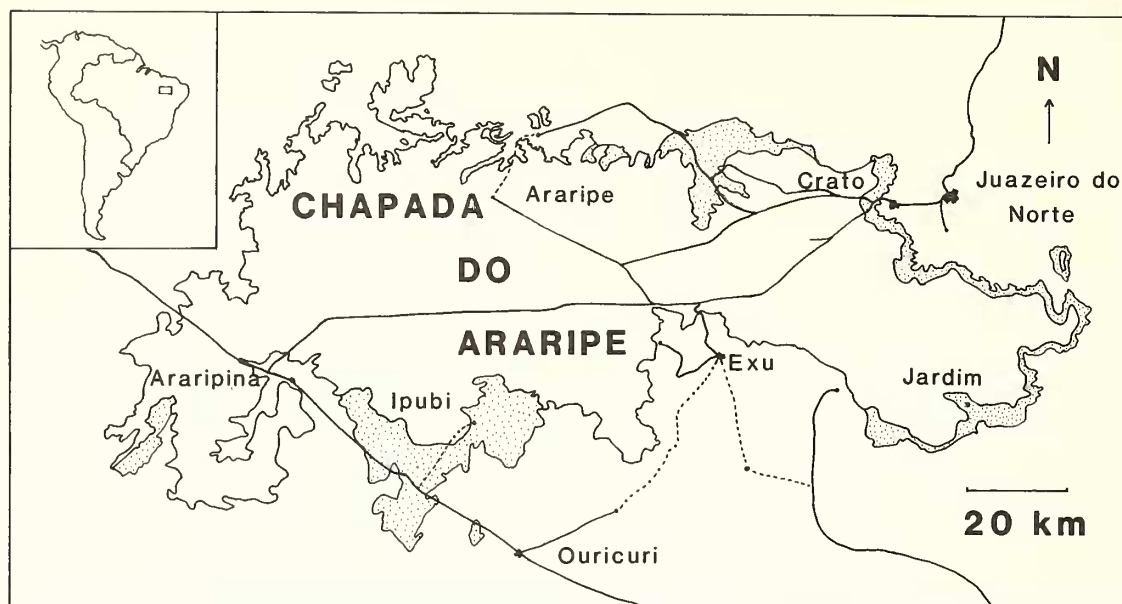
THE Santana Formation (?Upper Aptian) of the Chapada do Araripe, north-east Brazil, is one of the most important Cretaceous lagerstätten (*sensu* Seilacher *et al.* 1985), and has long been famous for the beautiful preservation of its fossil fish fauna. An examination of the large collections of Santana Formation fossil fishes at the Field Museum of Natural History, Chicago, the American Museum of Natural History, New York, and the British Museum (Natural History), London, suggests that soft-tissue fossilization in this formation is relatively common. In some fish specimens nearly the entire musculature of the trunk may be preserved, and in most of the three-dimensional specimens there is some phosphatization of soft tissues. Also, most of the specimens contained in calcareous concretions are only slightly compacted, and the three-dimensional shape of the specimen can frequently be determined.

Previous investigations of the fossil fishes have also revealed the presence of phosphatized soft tissues in associated ostracods (Bate 1972) and copepods (Cressey and Patterson 1973), while Campos *et al.* (1984) announced the discovery of pterosaurian wing membranes preserved in concretions from this formation.

The following work is based on observations made on over 300 fossil-bearing concretions held in the Field Museum of Natural History (FMNH), Chicago, the American Museum of Natural History (AMNH), New York, the British Museum (Natural History) (BMNH), London, and the University of Leicester (LEUG). Specimens used for destructive analysis were obtained from 'Rock Art', 4-6 Gypsy Lane, Leicester.

LOCALITY

The fossil-bearing concretions occur at a number of localities at the foot of the Chapada do Araripe, at the boundary between Ceara, Pernambuco, and Piaui provinces in north-east Brazil (see text-fig. 1). The Chapada lies between 7° and 7° 45' S. and between 39° and 41° W., forming an east-west trending plateau approximately 150 km long, with a general elevation of between 600 and 900 m above sea-level. The plateau consists largely of flat lying Cretaceous sediments lying unconformably on Devonian and Pre-Cambrian basement. Exposure is poor and restricted to a few stream sections and gypsum mines. Most of the fossil fish concretions are collected by local farmers or fossil dealers and sold to tourists at markets in São Paulo, or exported to foreign fossil dealers. There are restrictions controlling the export of large quantities of fossils from Brazil.



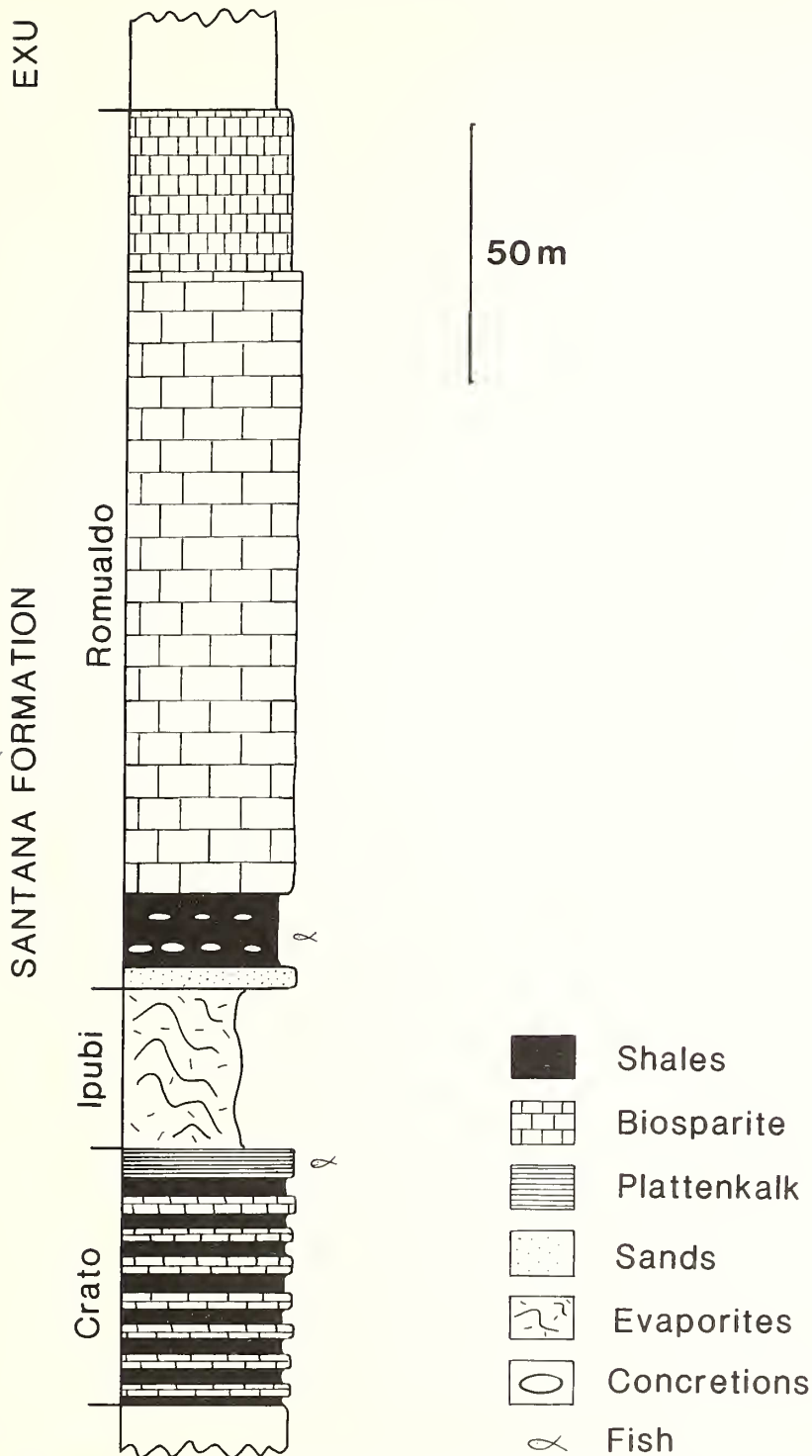
TEXT-FIG. 1. Locality map of the Chapada do Araripe, Brazil. Outcrop of the Santana Formation is indicated by light stipple.

STRATIGRAPHY

The fish-bearing concretions are from the Santana Formation of the Araripe Series. The main outcrop lies at the foot of the Chapada do Araripe, but a few small outliers occur to the south and west of the chapada. The stratigraphy of the Santana Formation has been examined by Beurlen (1962, 1963, 1971), Braun (1966), and Silva Santos and Valença (1967) and is generally considered to comprise three members (text-fig. 2). The lowest (Crato) member consists of a series of alternating shales and limestones (mainly biomicrites). At the top of the Crato Member a unit of finely bedded micrites (plattenkalk facies) yield abundant insects and the small fish *Distilbe elongatus* Silva Santos. This is overlain by a middle (Ipubi) member which is dominated by evaporites, including gypsum and anhydrite. The upper (Romualdo) member contains a variety of clays, limestones, and sandstone. Towards the base of the Romualdo Member there is a unit of bituminous shales and limestones (biomicrites) in which the fossil-bearing concretions occur.

The Brazilian Cretaceous is divided into a number of isolated basins which cannot be easily cross correlated. Due to the lack of diagnostic fossils in these basins the precise age of the Santana Formation is uncertain. Diagnostic marine invertebrates are almost unknown in the Santana Basin, and the vertebrates can only be used stratigraphically in a broad sense. Thus the age is considered to be Aptian or Lower Albian. Brito (1984) has proposed the erection of the *Vinctifer* Biozone to allow correlations to be made with other Brazilian Cretaceous basins. Unfortunately, the fish *Vinctifer* (= *Aspidorhynchus*) is a long ranging genus, and it is clear that its distribution is palaeoecologically controlled. The use of *Vinctifer* as a zone fossil must be treated with caution.

Sedimentation in the Brazilian Cretaceous basins was controlled by the separation of the South American and African plates, and the formation of the South Atlantic Ocean. Four distinct sedimentological episodes can be recognized (Bruto and Campos 1982, 1983). The lower part of the Santana Formation lies within the Alagoan (non-marine) Stage. The passage from non-marine to marine sediments is thought to approximate to the Middle Aptian/Upper Aptian boundary (Bruto 1984).



TEXT-FIG. 2. Simplified stratigraphic section through the Santana Formation of the Chapada do Araripe. Sedimentological data from Mabesoone and Tinoco (1973).

PALAEONTOLOGY

The Santana Formation is well known for the abundance and exceptional preservation of its contained fish fauna, the first records of which go back to the last century (Agassiz 1841, 1844; Gardner 1841; Woodward 1887) and early part of this century (Jordan and Branner 1908; Woodward 1908). The fish have received continued attention (Jordan 1923; D'Erasmus 1938; Schaeffer 1947; Silva Santos 1945, 1947, 1950, 1960, 1968, 1970*a, b*, 1974; Silva Santos and Valenca 1968; Campos and Wenz 1982) and are actively being studied as more taxa are being discovered. In recent years the Santana concretions have gained further importance for yielding amongst the worlds best-preserved pterosaur material. The pterosaurs were first described by Price (1971), and have been further investigated by Buissonje (1980), Campos (1983), Leonardi and Borgomanero (1983), Wellnhofer (1977, 1985), and Wellnhofer *et al.* (1983). Campos *et al.* (1984) reported a pterosaur in which wing membranes with supporting fibres are preserved. Other tetrapods reported from the Santana Formation concretions include crocodilians (Beurlen and Buffetaut 1981; Price 1959), turtles (Beurlen and Barreto 1968; Price 1973), and a possible dinosaur (Campos, D. de A. 1985).

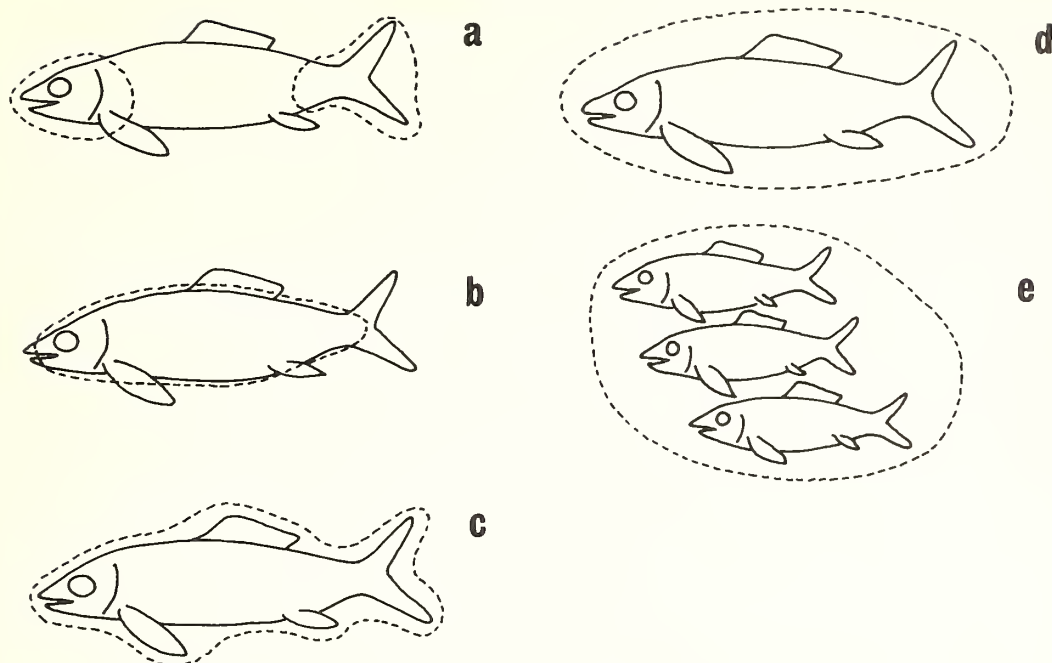
The invertebrate fauna is less diverse and there appears to be little information on the stratigraphic distribution of the various taxa. Smooth shelled ostracods are abundant in some of the fish-bearing concretions and occasionally copepods can be found. I have failed to observe any calcareous shelled invertebrates other than ostracods in the concretions. The invertebrate fauna of the formation as a whole has been reviewed by Lima (1979) and Mabesoone and Tinoco (1973). They list ostracods, decapod crustaceans (Beurlen 1963), and conchostracans, while Cressey and Patterson (1973) described the earliest known parasitic copepods. Gastropods, bivalves, and echinoids (Beurlen 1966) also occur. Recently, insects have been recorded from the top of the Crato Member (Maisey, pers. comm.) where rarely scorpions also occur (Campos, D. de R. B. 1985). The flora has been described by Lima (1978) and fossil resin is reported by Castro *et al.* (1970).

PALAEOECOLOGY

The palaeoecology of the various members of the Santana Formation has been discussed by Beurlen (1971), and by Mabesoone and Tinoco (1973). Most authors conclude that the various units of the Santana Formation show a trend from lacustrine (Crato Member), through restricted marine/evaporitic basin (Ipubi Member) to marginal marine environments (top of Romualdo Member). There is, however, little agreement on the environment of the concretion bearing horizon. Silva Santos and Valenca (1968) considered this level to be brackish on the basis of the contained fish fauna. Schaeffer (1947) thought the fish represented fully marine forms, while Beurlen (1971) suggested deposition under hypersaline conditions.

The salinity of the concretion bearing horizon is difficult to establish, and it is possible that surface water salinity differed significantly from that of the bottom waters. The fish fauna from the concretions contains forms that are well known from fully marine environments, including *Lepidotes* (Semionotidae), *Aspidorhynchus* [= *Vinctifer*] (Aspidorhynchiformes), *Microdon* (Pycnodontiformes), *Cladocycilus* (Ichthyodectiformes), and *Rhinobatos* (Rhinobatidae). Cressey and Patterson (1973) have demonstrated the presence of marine parasites on the gills of *Cladocycilus* sp. but considered also that the fish may have entered fresh water from the sea. The absence of a marine nektonic invertebrate fauna has led workers to consider that the concretion horizon must represent either fresh, brackish, or hypersaline conditions. Hypersaline conditions must be ruled out as the normal environment for the surface waters of the concretion horizon because of the diversity of the nektonic fish fauna, but an influx of hypersaline water may be considered as a possible mechanism for producing a mass mortality of nektonic organisms.

Mabesoone and Tinoco (1973) concluded that the concretions formed around fishes washed on to a palaeoshoreline by accretion of sediment on to an adipocere coated carcass. They argued that rolling around of the fish carcasses caused breakage of the distal portions of the fish fins, hence the common



TEXT-FIG. 3. Common morphologies of fish bearing concretions from the Santana Formation of north-east Brazil. *a*, formed around parts of skeleton only, based on FMNH PF 5493 and PF 8333. *b*, formed on body and skull only, most appendages remain outside concretion, based on FMNH PF 9778, PF 9669, and PF 9779. *c*, all of specimen enclosed within concretion, concretion shape reflects shape of fish, based on FMNH PF 10372. *d*, elliptical concretion envelopes entire fish, based on FMNH PF 9616, PF 9631, and PF 9632. *e*, concretion develops around several fish, based on FMNH PF 9625.

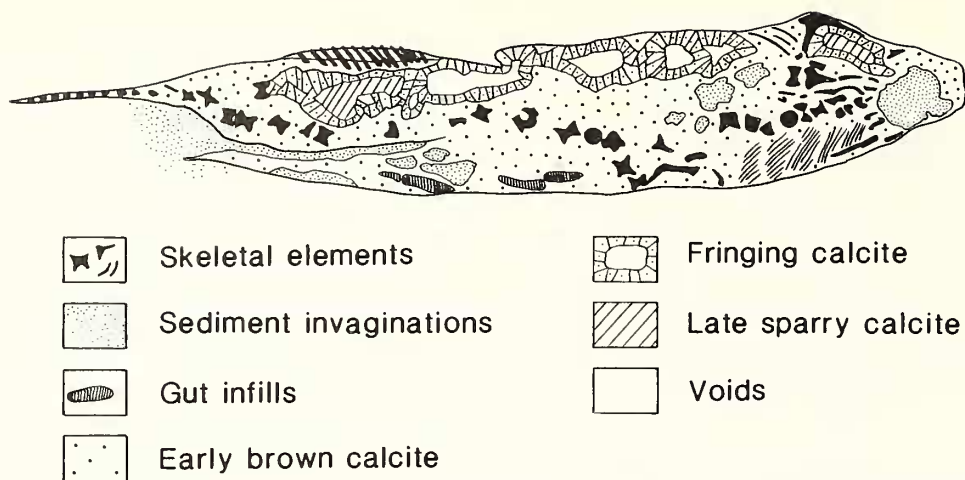
preservation of fish bodies only. A detailed investigation of the numerous concretions in the collections of FMNH, BMNH, and AMNH now show that this model cannot be accepted.

The concretions

The Santana concretions are subspherical bodies composed of laminated carbonate rich sediment, usually enclosing a vertebrate fossil (text-fig. 3). Unweathered concretions usually have a blue/grey core with an outer buff coloured zone. Weathered concretions are buff coloured throughout. The laminae appear as fine alternating light and dark bands varying in thickness from 1.00 mm to less than 0.25 mm. The sediment type varies between a poorly laminated ostracod biomicrite, to a micro-laminated calcareous clay, both with organic rich laminae. Laminae persist horizontally through the concretion, with slight attenuation due to compaction towards the edges. There is no evidence of accretionary accumulation of sediment comprising the concretion. In all of the concretions I have examined there has been a complete absence of benthic invertebrates except for ostracods, which are often present in vast numbers and probably of a single species. The ostracods are mostly articulated and filled with coarse sparry non-ferroan calcite.

Cements vary from sparry calcite in the ostracod rich bio-micrite concretions, to micro-spar in the calcareous clay concretions. All of the concretion cements are early diagenetic non-ferroan calcite.

Fracture within the concretions and void spaces within enclosed fossils are frequently filled with coarsely crystalline brown non-ferroan calcite. Larger voids within fossils occasionally show a late generation of ferroan calcite. Incompletely filled voids are lined with white rhombs of calcite approximately 1.00 mm across (text-fig. 4).



TEXT-FIG. 4. Cross-section through three-dimensional specimen of *Rhacolepis* sp., FMNH P12174, showing geopetal collapse of axial skeleton, upward development of gas cavities, and several generations of calcite cements.

Pyrite is abundant in unweathered concretions as patchily distributed crystal aggregates scattered throughout the concretion and lining cavities within trabecular bone. In some cases pyrite is found lining thin septarian cracks, and clearly pre-dates the non-ferroan calcite fills.

Phosphate occurs in some concretions as a replacement for soft tissues and as a surface coating of bones (the bones themselves are phosphatic, but this is original bio-genic phosphate and remains relatively unaltered) (Pl. 3, figs. 1-4). Phosphate also occurs in coprolites. The phosphate, a cryptocrystalline francolite, pre-dates all other diagenetic mineral phases. It is found replacing muscle fibres, some of which remain in myomeres (text-fig. 5). Some myomers clearly began to decompose before phosphatization occurred and appear as a mass of disordered muscle fibres (see Pl. 1, figs. 2 and 3). A vertical thin section of *Notelops brama* (AMNH 11753, Pl. 4, fig. 5) shows the upper surface of the specimen is devoid of scales. Body segments of muscle fibres (myomeres) are preserved in phosphate, and are in direct contact with the overlying sediment. Thus, phosphatization must have occurred prior to burial, as no sediment has invaded the exposed body cavity or tissues. This is strong evidence that phosphatization occurred extremely early.

Accessory minerals within the concretions include sphalerite, which is usually associated with bone, baryte, and malachite, the latter probably being derived from a sulphide precursor.

Sections through concretions containing fishes with ruptured body walls, reveal gas escape structures through the concretion. These emanate from the body cavity of the fish. In some the body wall of the fish has parted from the enclosing concretion as the gas pressure within the fish was released (Pl. 4, fig. 1a, b). There is some plastic deformation of the sediment above the gas cavity due to this pressure release. Rarely, small quantities of sediment have invaded the body cavity of some

EXPLANATION OF PLATE I

Figs. 1-4. Carbonate concretions with fish from the Santana Formation (?Aptian), Brazil. 1, *Brannerion vestitum* Jordan and Branner, FMNH PF 9607, specimen showing preservation of entire trunk musculature in intact myomeres, $\times \frac{3}{4}$. 2, *Notelops brama* (Agassiz), AMNH 11753, muscle fibres preserved, but intact myomeres restricted to central core of trunk, $\times \frac{1}{2}$. 3, *N. brama* (Agassiz), FMNH PF 9626, all muscle fibres preserved, but no myomeres remain intact, $\times \frac{3}{4}$. 4, *Rhacolepis* sp., FMNH PF 10771, multi-specimen concretion with orientated, articulated fish, $\times \frac{3}{4}$.



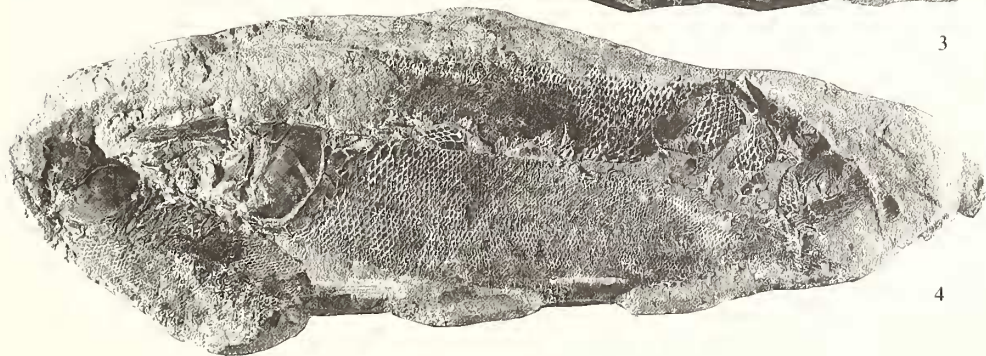
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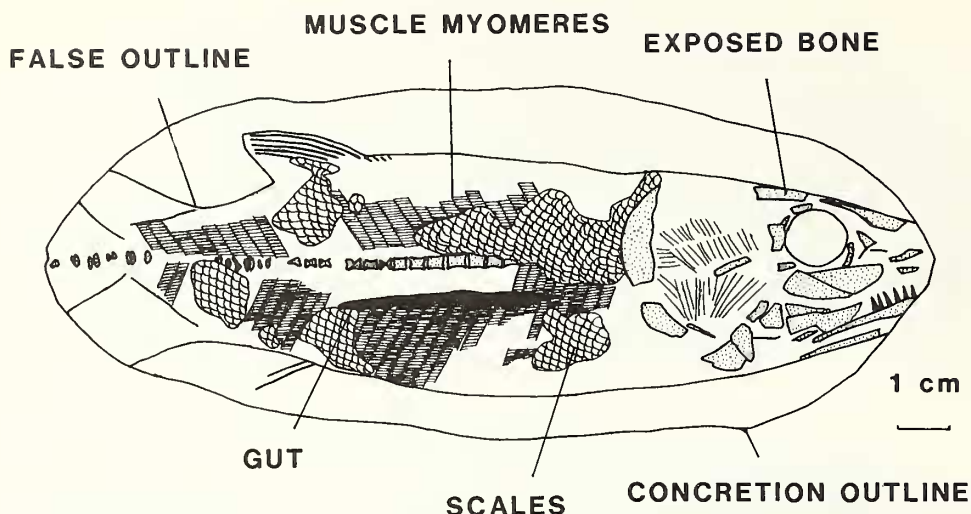
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TEXT-FIG. 5. Diagrammatic representation of *Brannerion vestitum* Jordan and Branner, FMNH PF 9607 (see also Pl. 1, fig. 1), showing musculature preserved in myomeres. Note the outline of the fish is an artefact of the preparator as indicated by the posterior continuation of the axial skeleton beyond the outline of the 'caudal fin'.

specimens. More commonly, the surrounding sediment has remained intact with little or no invasion of the body cavity, indicating some coherence of the sediment at a very early stage. Slight compaction of the sediment within the concretion around enclosed fossils is indicated by the draping over of laminae.

The formation of concretions began during the decomposition of the vertebrate carcasses. Gas pressure within the carcasses allowed small (up to 40 cm) fishes with intact body walls to remain three-dimensional until the surrounding sediment had become partly lithified. The sediment probably behaved like a stiff gel.

Eventually gas pressure within the body cavity increased sufficiently to explode from the body cavity. The sediment was soft enough to allow upward escape of the gas, but was sufficiently firm to resist collapsing into the cavity of the fish. The diagenetic history of concretion formation is summarized in text-fig. 6.

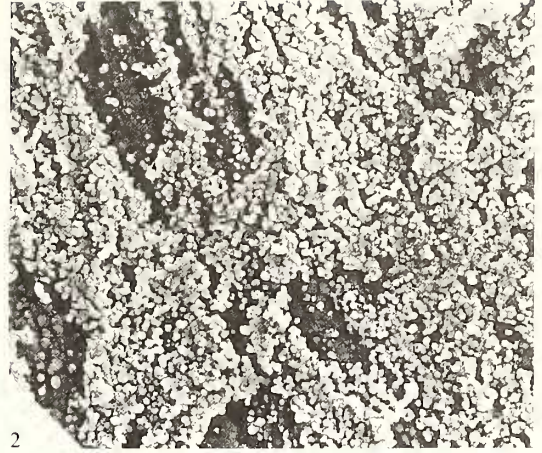
In many fish specimens, scales from the upper surface of the fish have become detached and lie a few millimetres from the carcass. This indicates that the fish must have begun to decompose while lying exposed on the sea floor. Under normal conditions, a carcass exposed for only a few days would be scavenged or dispersed by current activity. Low oxygen levels may have reduced scavenging to a minimum, but the abundance of articulated ostracods indicates well-oxygenated bottom water was present. Current activity must have been almost zero as even the smallest of fish scales and fin rays

EXPLANATION OF PLATE 2

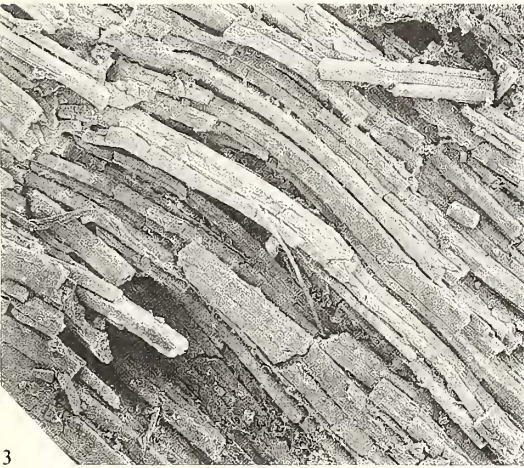
Figs. 1–6. Muscle preservation in Brazilian teleost fishes. 1, *Brannerion vestitum* Jordan and Branner, FMNH PF 9607, intact muscle myomeres with well-preserved muscle fibre, $\times 7$. 2, SEM of muscle fibres from *Rhacolepis* sp. prepared in dilute acetic acid, BMNH P62145, $\times 80$. 3, surface detail of fig. 2 showing granular texture produced by masses of phosphatic spherulites, $\times 615$. 4, rib of *Rhacolepis* sp. with surface coating of phosphatic spherulites, $\times 780$. 5, mass of phosphatic spherulites replacing muscle fibre of *Rhacolepis* sp., $\times 12000$. 6, detail of phosphatic spherulites showing individual lath-like crystallites, $\times 64000$.



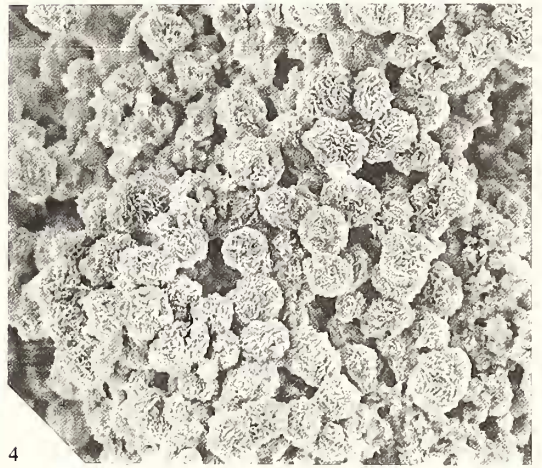
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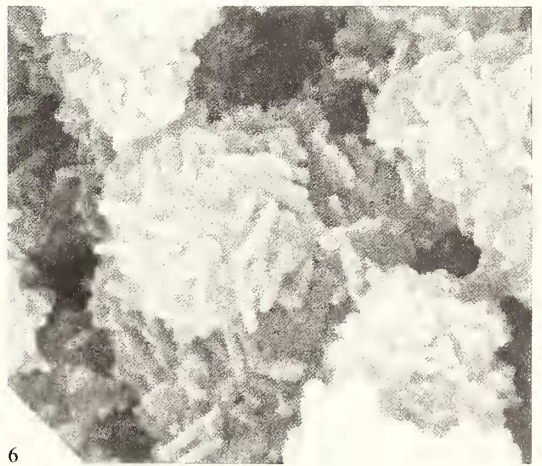
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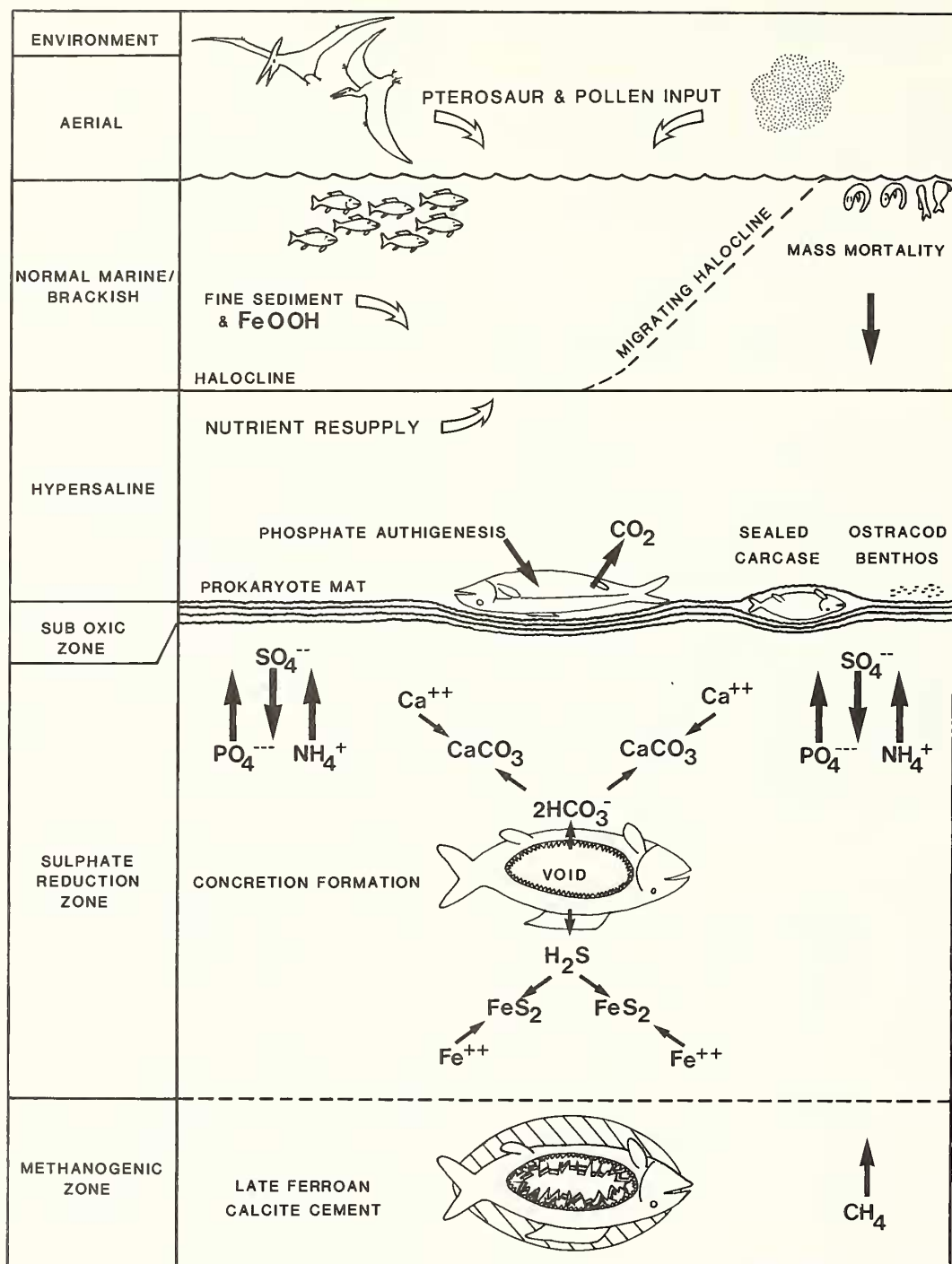
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TEXT-FIG. 6. Geochemical model for the mass mortality of the Santana biota and the preservation of soft tissues by phosphate authigenesis under oxic conditions.

remain articulated, and detached scales only lie a few millimetres from the main portion of the carcass. The few separated scales were presumably detached due to the early escape of decomposition gases.

Cypridid ostracods have been used by Bate (1972) to show that the fauna is non-marine, but marine cypridid ostracods are known (e.g. *Suzinia*, Moore 1961). Bate (1972) also considered that the ostracods must have been feeding on the fish carcasses, but thin sections through ostracod bearing fish containing concretions show that ostracods were present in the sediment before and after the fish carcasses arrived on the sea floor. No ostracods occur within the body cavity of the fish. The general lack of other benthic organisms in the concretions may be due to diagenetic removal, but most likely the restricted benthos was the result of slightly hypersaline bottom water.

EODIAGENETIC ENVIRONMENT

Prior to the event which killed large numbers of fishes in the Santana basin, bottom waters were probably well oxygenated and hypersaline. Organic rich laminae within the concretions indicate the presence of a widespread prokaryotic mat covering the sea floor. Presumably such an extensive mat could survive due to a lack of grazing invertebrates inhibited by the hypersaline water. A similar situation has been postulated for the Solnhofen Limestone (Jurassic) of Germany (Keupp 1977). The mat may also have had a role in restricting colonization of the sea floor by hypersaline tolerant infauna and epifauna, but provided a suitable substrate for salt tolerant ostracods.

After the mass mortality of fishes living at all levels in the water column, many thousands of fishes descended to the sea floor. It is also likely that many floated for a prolonged period and drifted away from the area of the event to be washed on to nearby shores, as happens from time to time on the west coast of Africa (Brongersma-Sanders 1949).

Many of the fish carcasses that descended to the sea floor may have been overgrown by the prokaryotic mat, or became entangled in it by their fins. This would prevent the carcass from rising to the surface as decomposition gases slowly built up inside the body cavity.

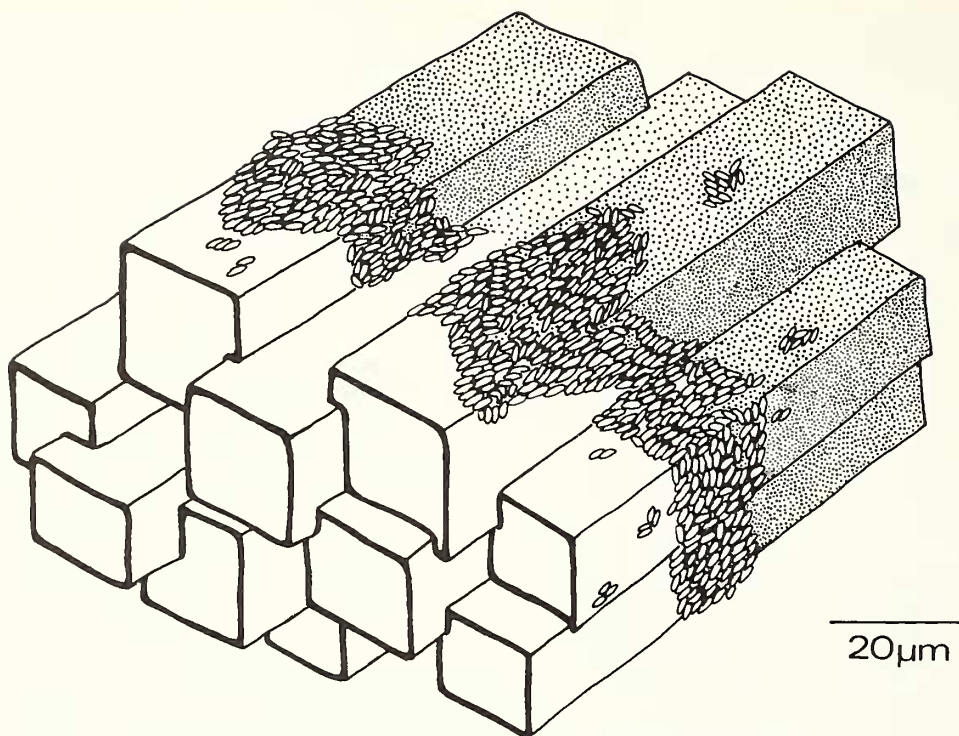
The accumulation of vast numbers of fishes on the sea floor undergoing decomposition may have rapidly depleted the level of dissolved oxygen in the water column. The bottom water, especially adjacent to the carcasses may have become anoxic. This could have the effect of killing the benthic ostracods, and of inhibiting continued growth of the prokaryote mat.

The presence of a mat trapping a carcass may have allowed the build up of a variety of decomposition products. If CO_2 was allowed to build up initially, the pH of the environment immediately surrounding the fish would decrease slightly. This would have two major effects, first to inhibit carbonate precipitation, and secondly to enhance the precipitation of francolite. Low pH may also have been maintained by the oxidation of sulphides migrating upwards from the sulphate reduction zone (Coleman 1985).

Phosphate is relatively rare in sea water, but it builds up in sediment pore waters due to microbial breakdown of organic material (Berner 1980). Concentrations of phosphate in the sediment increase with depth, and a concentration gradient exists between the deeper buried sediment and the sediment/water interface. Thus, dissolved phosphate diffused into the carcasses both from the sea water and from pore water. This and additional phosphate, liberated by bacteria feeding on proteins, RNA (Lucas and Prevot 1984), and other phosphorous rich bio-molecules within the carcass was unable to remain in solution, and was rapidly precipitated as francolite micro-spheres (text-fig. 7). Presumably larger authigenic crystals did not grow due to the presence of inhibitory magnesium (McConnell 1973).

This initial low pH micro-environment persisted only briefly, and was brought to an end by the production of vast amounts of ammonia which rapidly increased the pH of surrounding waters. In this way phosphatization of the soft tissues took place within a few seconds of the bacteria metabolizing the tissue (see text-fig. 5), and probably only a few hours after the dead fish arrived on the sea floor.

Phosphatization of soft tissues did not take place in all of the fish specimens, but in most specimens the same type of phosphate occurs on bone surfaces. Petrographic study of the bone suggests that no



TEXT-FIG. 7. Diagrammatic representation of muscle fibre bacterial breakdown, with subsequent replacement of fibres by francolite micro-spheres, scale bar 20 μm .

alteration of the bone has taken place, and therefore bone phosphate has not been a source of phosphate for the preservation of the soft tissues.

In some of the fish specimens (Pl. 1, figs. 2–4) almost the entire musculature of the trunk has been preserved. It is difficult to see how so much phosphate can be rapidly dumped unless vast quantities of phosphate-enriched pore water are flushed through the system. It is equally difficult to explain why some specimens have no soft tissues preserved at all, although this latter observation may be due to derivation of concretions from different localities.

During the initial phase of decomposition with accompanied phosphatization, sedimentation continued. Further decomposition beneath a few millimetres of sediment by anaerobic bacteria (sulphate reducers), continued to liberate ammonia which maintained high pH in pore water and created an environment for the early precipitation of carbonate to begin concretion formation. This prevented compaction of the smaller fish under the increasing weight of overburden.

EXPLANATION OF PLATE 3

Figs. 1–4. Soft tissues from Brazilian Cretaceous teleost fishes. 1, *Rhacolepis* sp., LEIUG 94515. *a*, secondary lamellae of gills attached to gill ray, $\times 50$; *b*, oblique view of secondary lamellae, $\times 100$; *c*, detail of surface of secondary lamellae displaying rope-like texture, $\times 930$. 2, *Rhacolepis* sp. Phosphatized stomach wall, removed from BMNH P62101. SEM stub now LEIUG 94516. *a*, portion of stomach wall, $\times 30$; *b*, detail of reticulated surface, $\times 200$. 3, possible nerve fibre entering section of fibrous muscle, $\times 300$, LEIUG 94517. 4, ?phosphatized bacteria on surface of fish bone, $\times 59\,600$.

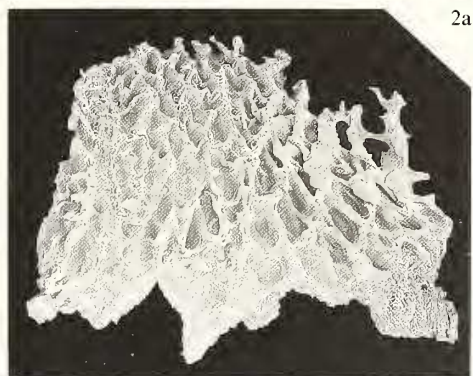
All photographs are of acetic acid prepared specimens.



1a



1b



2a



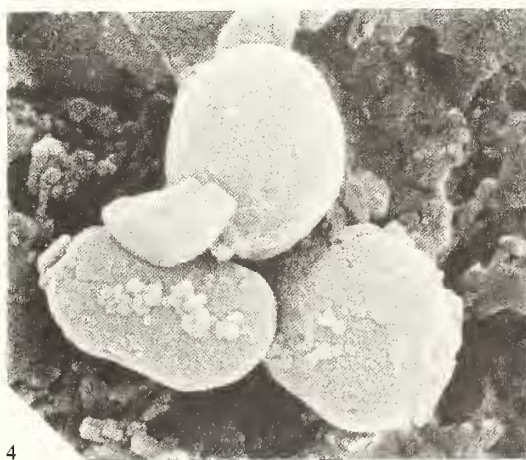
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Subsequent burial of the fish carcass passed it from an oxidizing or suboxic zone to the sulphate reducing zone. Here precipitation of iron monosulphides with later conversion to pyrite assisted in cementing the surrounding sediment, and produced authigenic pyrite on the surfaces of bones. At the same time precipitation of non-ferroan carbonates centripetal to the carcass formed pre-compaction concretions with non-ferroan sparry calcite void fills. With increased depth of burial the concretion enclosed carcass passed into the methanogenic zone. Continued calcite precipitation in voids within the body cavity produced fringes of ferroan calcite, but no ferroan calcite was precipitated on the fringes of the concretions, possibly because the pH was too low beyond the concretion limits.

MASS MORTALITY

The great abundance of fish at the concretion horizon(s) of the Santana Formation is suggestive of one or more mass mortality events. The number of concretion horizons within the Romualdo Member is not recorded, but it is likely that there are several concretion bearing layers over the area of the outcrop. Most concretions contain only a single fish skeleton, but a few concretions contain several fish (Pl. 1, fig. 4), often of the same taxon, and of similar size. This is suggestive of the death of an entire shoal rather than the accumulation of individual fish killed in separate events through time.

The cause of the mass mortality events cannot easily be established, but it seems likely that a catastrophic change of chemistry or temperature could have occurred in the surface water. In marginal marine environments changes in salinity may occur relatively fast. An upward migration of the halocline to the surface could result in the sudden death of organisms in the nekton. Sudden changes of temperature in surface waters periodically kill vast numbers of fishes in the Gulf of Mexico (Gunter 1947), as can blooms of surface living micro-organisms (Brongersma-Sanders 1949), either by clogging the gills and causing asphyxiation or by producing toxins in the water column.

DISCUSSION

The importance of prokaryotic scums on sediment surfaces is not yet fully appreciated, but it is becoming clear that thin microbial films of cyanobacteria play an important physical and biochemical role in sediment diagenesis and fossilization processes. In the finer grained Santana Formation concretions, fine carbonaceous laminae lie between equally thin microcrystalline calcareous laminae. Sheets of this carbonaceous material can easily be extracted from the concretion by dissolution in dilute acetic acid. The thin sheets are dark brown, amorphous flakes which resemble modern dead bacterial scums found on dried lake beds. Some poorly preserved filaments can be seen after treatment of the mat with concentrated nitric acid.

Such microbial films play two important roles. First, they prevent colonization of the sea floor by epibenthos and endobenthos (Keupp 1977) and as a result protect the sediment from bioturbation, and secondly, such mats provide a plentiful source of organic matter for feeding autotrophic bacteria

EXPLANATION OF PLATE 4

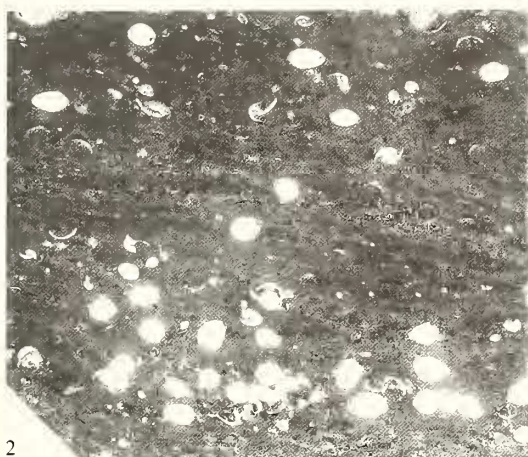
Figs. 1-5. Thin sections of Santana Formation concretions. 1a, section through three-dimensional specimen of *Rhacolepis* sp. showing geopetal collapse of axial skeleton (black arrow) and gas escape structure. The thin laminae above the fish have collapsed as gas escaped, FMNH PF 10765, $\times 1.8$. 1b, detail of gas escape structure in same specimen showing fringing calcites, $\times 4.5$. 2, section through laminated concretion showing numerous articulated cypridid ostracodes, FMNH PF 11846a, $\times 10$. 3, section through vertebral centra of a flattened *Enneles* sp. showing that despite flattening the bone has remained uncrushed, FMNH PF 11846a, $\times 10$. 4, stained section through cavity in trunk of *Rhacolepis* sp. showing several generations of carbonate cement and euhedral calcite crystals lining the cavity, FMNH PF 10765, $\times 5$. 5, phosphatic fringes on surface of bone in *Notelops brama*, AMNH 11753, $\times 10$.



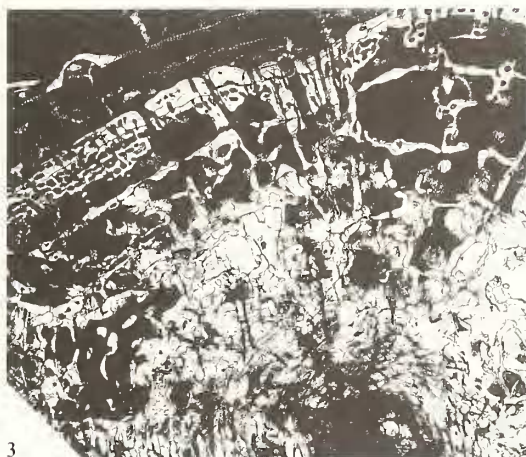
1a



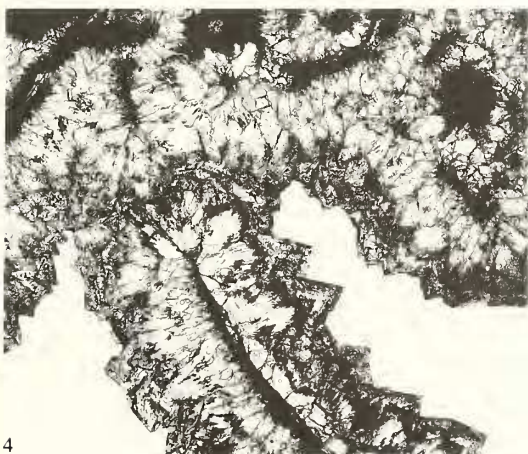
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within the sediment. Consequently, they may fuel complex diagenetic reactions. In the Santana Formation such reactions have enabled delicate soft tissues to be preserved in a three-dimensional state.

Seilacher *et al.* (1985) point out that today cyanobacterial films are mainly restricted to hypersaline environments. The low diversity of the Santana benthos (mainly smooth shelled ostracods) may be due to increased salinity; thus a partly stratified water column with hypersaline bottom water may have existed within the basin, which could be used to explain the rarity of largely benthonic fish such as *Rhinobatos* and the mollusc eating pycnodonts. This palaeoecological model should be used to assist in the discovery of other sites of exceptional fossil preservation.

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